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MILLIPEDS OF THE SIGMORIA LATIOR COMPLEX (POLYDESMIDA:XYSTODESMIDAE)[1]

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The milliped genus *Sigmoria* is one of the most heterogeneous in the family Xystodesmidae. Proposed by Chamberlin (1939) and summarized by Hoffman (1950) and Chamberlin and Hoffman (1958), the genus is characterized by a male gonopod with the telopodite bent distally into a sigmoid curve. Hoffman (1958) stated that it had become a 'catch all' genus for xystodesmids not readily conforming to other genera and suggested a possible criterion for *Sigmoria*, but a generic revision is still many years away. The fourteen species which comprise the genus present a bewildering variety of forms with little but the sigmoid curvature in common. Five species, however—*S. latior* (Brölemann, 1900); *S. aberrans* Chamberlin, 1939; *S. conclusa* Chamberlin, 1939; *S. marionа* Chamberlin, 1939; and *S. furcifera* Hoffman, 1949—share the common feature of a medial expansion (flange) at midlength of the telopodite. The last species was described from near Pineville, West Virginia; the others were originally reported from North Carolina localities and listed by Wray (1967).[2]

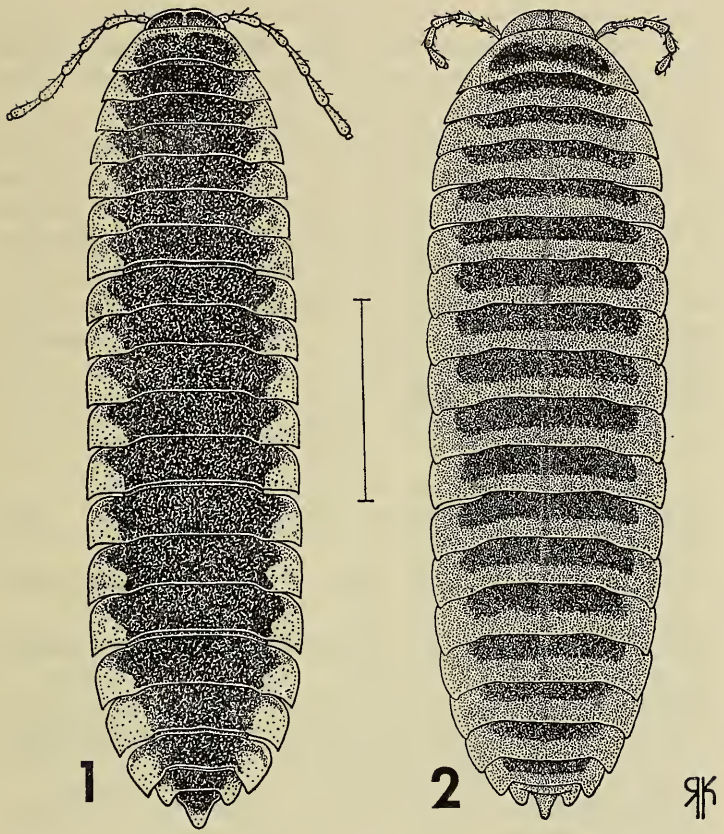
My interest in these xystodesmids began with the collection of an individual from William B. Umstead State Park, Wake Co., North Carolina. Subsequent discoveries in Johnston, Moore, and Wilkes Cos. indicated that the form was widely

[1] Contribution No. 2, North Carolina State Museum of Natural History.
[2] Chamberlin (1939) reported the type locality of *S. conclusa* as being "Tennessee:Altapass." However, Hoffman (1950) corrected the error by stating that this locality was actually in Mitchell County, North Carolina.

distributed across the northern half of the state, and upon examination of available museum material, I discovered that it actually extends into southern South Carolina. Two distinct color patterns are evident (Figs. 1, 2), but all individuals are otherwise similar externally. The average W/L ratio is 26.3% and is relatively constant throughout the range. The male gonopods, however, are highly variable in terms of the size and shape of the flange, the shape of the prefemoral process, and the presence or absence of a subterminal tooth on the telopodite. In assessing the pattern of this variation throughout the range (Fig. 17), it is apparent that the existence of five separate species can no longer be justified. In three regions (not four as stated by Shelley (1975a)), the frequency of certain gonopodal characters indicates that the populations are sufficiently distinct to be designated as subspecies, but nowhere is there sufficient reason to name more than one full species. Since S. *latior* is the oldest available name, it is retained as the single species represented by this flanged form. The population previously represented by S. *mariona* warrants distinction as a subspecies, and an undescribed subspecies occurs in southern South Carolina. The other three species—S. *aberrans*, S. *conclusa*, and S. *furcifera*—are identical with the nominate subspecies. Intergrades of variable characteristics occur in the intervening area between the three subspecies.

The taxonomically important characters in the S. *latior* complex involve chiefly the male gonopod, although color pattern is of limited value (see distribution section). Specific aspects of the gonopod that are diagnostically important include the size and shape of the flange, degree of development of the subterminal tooth, conformation of the telopodite distad to the tooth, overall length and degree of angulation in the prefemoral process, and presence or absence of bifurcation.

Due to the subtle gonopodal differences between subspecies and intergrades, only the identity of mature males can be accurately established. The male gonopod is also the most reliable determinant for distinguishing this complex from other xystodesmids. Female xystodesmids are easily misidentified, even to genus, and a female with a seemingly



Figs. 1–2. Color patterns in *Sigmoria latior.* 1, metaterga solid black in color, without stripes, displayed in northern half of range by *S. l. latior.* Specimen is a male from Rendezvous Mtn., Wilkes Co., North Carolina (NCSM 1854). 2, striped color pattern (metaterga with stripe along caudal edge connecting with paranota) displayed in southern half of range by *S. l. mariona, S. l. hoffmani,* and all intergrades. Specimen is a male *S. l. latior* × *S. l. hoffmani* intergrade from 3.7 mi. SW Wagram, Scotland Co., North Carolina (NCSM 2538). Scale line = 1.0 cm for Fig. 1 and 0.75 cm for Fig 2.

appropriate color patern does not necessarily belong in the *S. latior* complex. Consequently, literature records based on females alone cannot be considered reliable. In the course of this study, I have examined over 120 specimens, but only

samples with at least one mature male were considered. The range and distribution patterns, therefore, are those of adult males. Expansion of the ranges by the acquisition of further male specimens is likely in the future.

The nomenclatorial rearrangement of these flanged diplopods is carried out herein. A full description is presented for the nominate subspecies, and diagnostic characters are detailed for the others. A key is presented to facilitate identification. The range of each subspecies and intergrade combination is discussed along with specific locality records, and the overall distribution of the complex is summarized. Ecological observations are also reported.

Abbreviations used in the text to designate the sources of preserved study material are as follows:

CM—Carnegie Museum, Pittsburgh, Pennsylvania.
MNHP—Museum National d'Histoire Naturelle, Paris, France.
NCSM—North Carolina State Museum, Raleigh, North Carolina.
RLH—Private collection of Richard L. Hoffman, Radford, Virginia.
RVC—Private collection of the late Ralph V. Chamberlin, now being accessioned by the United States National Museum.
USNM—United States National Museum, Washington, D. C.

Acknowledgments

As with most papers on millipeds of the southeastern U. S., Leslie Hubricht deserves primary recognition for his field collections. More specimens of the *S. latior* complex have been secured by him than by any other collector, and the present picture would certainly not have emerged without his outstanding field work.

Additional collectors, too numerous to list, also contributed one or a few specimens. Each is cited after the respective collection in the text. In this regard, I add my thanks to the North Carolina Department of Natural and Economic Re-

sources, Division of State Parks, for permission to collect in the North Carolina State Parks.

For the privilege of examining the types of *Fontaria latior* and *Sigmoria furcifera* respectively, I gratefully acknowledge the assistance of J. P. Mauries, Museum National d'Histoire Naturelle, Paris, France, and Ralph E. Crabill, Jr., U. S. National Museum. Specimens from the Carnegie Museum were kindly loaned by George E. Wallace.

I am deeply indebted to Richard L. Hoffman, who collected many specimens himself and generously loaned me his entire collection, containing most of the available material. Dr. Hoffman also contributed valuable comments and suggestions on the manuscript. Figures 1 and 2 were prepared by Renaldo G. Kuhler, N. C. State Museum staff artist; the other illustrations are the work of the author.

KEY TO THE SUBSPECIES OF SIGMORIA LATIOR (BASED ON ADULT MALES)

1. Telopodite of male gonopod with subterminal tooth on medial edge distad to flange; metaterga with or without yellowish stripe along caudal edge 2

   Telopodite of male gonopod without subterminal tooth on medial edge distad to flange; metaterga with yellowish stripe along caudal edge; eastern slope of mountains of southwestern North Carolina .....*latior mariona Chamberlin*

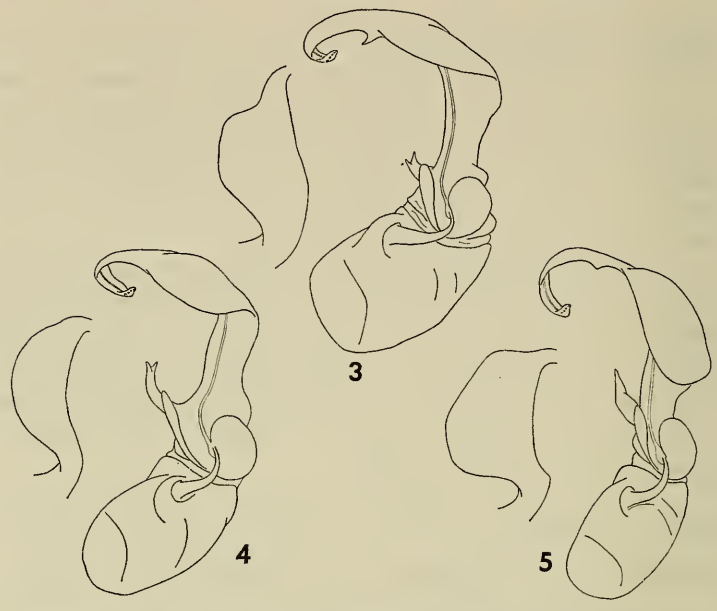
2. Prefemoral process simple or with varying bifurcation; flange moderate, at maximum depth well above level of prefemoral process (medial view), subequal in depth to that of distal curvature of telopodite; distal curve of telopodite narrow, beginning closer to tip than to subterminal tooth; metaterga solid black in color, without stripe along caudal edge; northern North Carolina to southern West Virginia .....*latior latior* (Brölemann)

   Prefemoral process simple, never bifurcate; flange greatly enlarged, extending at maximum depth to level of prefemoral process (medial view), greater in depth than that of distal curvature of telopodite; distal curve of telopodite broad, usually beginning closer to subterminal tooth than to tip; metaterga with yellowish stripe along caudal edge; coastal plain of southern South Carolina .....*latior hoffmani* new subspecies

Sigmoria latior latior (Brölemann), new status

Figures 3, 6–14

Fontaria latior Brölemann, 1900, p. 123, pl. 6, figs. 37–42.
Apheloria latior Attems, 1938, p. 168.



Figs. 3–5. Left male gonopods of *Sigmoria latior* subspecies (medial view) with direct view of flange. 3, *S. l. latior*, specimen from 4 mi. SE Jonas Ridge, Burke Co., N. C. (RLH). 4, *S. l. mariona*, holotype, specimen from Marion, McDowell Co., N. C. (RVC). 5, *S. l. hoffmani*, holotype, specimen from 4.4 mi. NW North, Orangeburg Co., S. C. (RLH).

Sigmoria latior Hoffman, 1950, p. 5—Chamberlin & Hoffman, 1958, p. 50.—Wray, 1967, p. 152.

Sigmoria aberrans Chamberlin, 1939, p. 8, pl. 3, figs. 24, 25.—Hoffman, 1950, p. 2.—Chamberlin & Hoffman, 1958, p. 49.—Wray, 1967, p. 152. [New synonymy.]

Sigmoria conclusa Chamberlin, 1939, p. 8, pl. 3, figs. 22, 23.—Hoffman, 1950, p. 4.—Chamberlin & Hoffman, 1958, p. 49.—Wray, 1967, p. 152. [New synonymy.]

Sigmoria furcifera Hoffman, 1949, p. 387, pl. 27, figs. 17, 18.—Hoffman, 1950, p. 4.—Chamberlin & Hoffman, 1958, p. 50. [New synonymy.]

Type-specimen: Male holotype (MNHP) collected from "North Carolina" without additional data. The collector is unknown, and the specimen was originally housed in the collection of E. Simon, who later gave it to Brölemann. Having examined this specimen, I can now report

that it came from the region of intergradation in south-central North Carolina, and the type-locality is thus restricted to the region south of the Deep-Cape Fear Rivers. Of the material available to me, it conforms most closely to a male from Raeford, Hoke Co. (RLH), but is sufficiently different to prohibit further specification of the probable locality. The subspecies in northern North Carolina, to which the specimen is closest morphologically and geographically, is hereby considered the nominate subspecies.

Although Brölemann's specimen must remain the holotype, the range of the nominate subspecies is here restricted to the region north of the Deep-Cape Fear Rivers, and therefore a more "typical" male has been selected for redescription. This individual was collected by R. L. Hoffman, 11 July 1962, 4 mi. SE Jonas Ridge, Barkhouse Recreation Area, Burke Co., North Carolina (RLH).

Diagnosis: Metaterga without stripes along caudal edge, solid black in color; paranota varying from red to yellow in color; male gonopods with following characters: prefemoral process short, bent at midlength into approximately a right angle, simple or bifurcate; flange moderate, extending (medial view) only as low as tip of telopodite; subterminal tooth present, subtriangular; distal curvature of telopodite beginning much closer to tip than to tooth, forming arc with relatively narrow diameter.

Description: Given in full only for the nominate subspecies, the others differing only in color pattern and gonopod structure.

Length 42.6 mm, maximum width 11.1 mm, W/L ratio 26.1%. Color in life: paranota bright lemon yellow, metaterga black; yellow stripe along anterior edge of collum, connecting with paranotal spots; epicranium dark brown, suture white; frons and genae light brown, clypeus yellow; antennae yellow, ultimate and penultimate segments brown; venter white; legs white basally, other podomeres yellow, claws and distal end of tarsi brown.

Head capsule smooth, polished; epicranial suture thin but distinct; antennae moderately long and slender, reaching back to middle of paranota of third segment and becoming progressively more hirsute distally; first antennomere subglobose, 2–6 clavate, 7 short and truncate; genae not margined laterally, genal apices projecting slightly beyond adjacent margins of cranium.

Terga smooth, polished; paranota depressed, continuing slope of dorsum, damaged on right side of segments 2–4; anterior corners of paranota rounded; posterior edge of paranota continuous with that of metaterga on segments 1–11, becoming angled at 12 and progressively more so caudally; peritremata thick and conspicuous, sharply set off from paranotal surface, produced slightly caudad beginning on segment 7; ozopores opening dorsally, located in middle of peritremata.

Pregonopodal sterna unmodified except for pair of small, paramedial knobs between 4th pair of legs; postgonopodal sterna produced into

small, blunt lobes subtending both pairs of coxae on segments 8–16; sternal surface smooth, glabrous, slightly depressed between lobes on caudal edge. Pregonopodal legs densely hirsute; postgonodal legs becoming progressively less hirsute caudally; small coxal spine present on legs of segments 9–17. Hypoproct rounded; paraprocts with margins strongly thickened.

Gonopodal aperture elliptical, indented on antero-lateral margin; edges slightly raised. Gonopods (medial view) with prefemoral process short, bifurcate, vertical component slightly longer and thicker than horizontal component, bent at nearly a right angle at midlength (juncture of two components); flange extending nearly as low as tip of telopodite, well above level of prefemoral process; subterminal tooth sharply pointed, distinct; telopodite angled slightly downward distad to tooth; distal curve of telopodite forming arc with relatively narrow diameter, beginning of curve proximal to tip, much closer to tip than to subterminal tooth.

Variation: All specimens seen in life (or with color notations) have solid black metaterga (without stripes), but the color of the paranota and stripe along the anterior edge of the collum may vary. Individuals from Wilkes Co., North Carolina, were red (NCSM 1854) and orange (NCSM 1826), while those from Johnston and Wake Co., in the eastern piedmont, were yellow (NCSM 1557, 1704). A specimen with red paranota from Roaring Gap, Alleghany Co., North Carolina, was illustrated by Levi, Levi, and Zim (1968, p. 149). Aside from color, there is little difference in the non-gonopodal characters.

On the gonopods, however, the prefemoral processes vary considerably. They may be simple or bifurcate, with either component longer and more prominent than the other (Figs. 6–14). Regardless of the relative lengths of the components, the angle between the vertical component and the base of the process is approximately a right angle. The overall length of the process is about the same in all individuals, but seems to be slightly longer in those which lack bifurcation.

The other gonopodal characters vary little from the condition described above for the Burke Co. specimen. The subterminal tooth is slightly reduced and rounded on individuals from Buchanan, Washington (3 miles NE Mendota), and Grayson Cos., Virginia, but otherwise it is distinct and subtriangular. The distal curve of the telopodite is much closer to the tip than to the tooth, but the distance between the curve and tooth is greater in some individuals. In all specimens, the flange (medial view) is subequal in depth to that of the distal curvature of the telopodite.

Distribution: This subspecies spans elevations of approximately 300–3000 ft. in North Carolina, southwestern Virginia, and southern West Virginia, and includes localities previously reported for *S. aberrans* and *S. conclusa* (Hoffman, 1950; Chamberlin & Hoffman, 1958; and Wray, 1967) and *S. furcifera* (Hoffman, 1949, 1950; and Chamberlin

Figs. 6–14: Variation in prefemoral processes of S. *l. latior* (medial view), localities as follows: 6–10, five individuals from Rendezvous Mtn., Wilkes Co., N. C. (NCSM 1854). 11, near Pineville, Wyoming Co., W. Va. (USNM 1809). 12, 8 mi. SE Blowing Rock, Caldwell Co., N. C. (RLH). 13, William B. Umstead State Park, Wake Co., N. C. (NCSM 1704). 14, near summit of Clinch Mtn., Washington Co., Va. (RLH).

& Hoffman, 1958). Known range extremes include the Ohio River drainages of southern West Virginia in the north and west and the upper Neuse River basin of North Carolina in the east. No specimens have been encountered in the Tar or Roanoke basins in either North Carolina or Virginia. In North Carolina, the range extends as far south as the Catawba River in the western piedmont and mountains and the Deep-Cape Fear Rivers in the eastern piedmont; no specimens have been collected in the coastal plain.

The subspecies appears to be a valley form in montane regions, as suggested by Hoffman (1950). The highest known elevation is 3018 ft., near the summit of Clinch Mountain, Washington Co., Virginia. The Clinch Mtn. specimens are also the only representatives of the subspecies known authentically from regions which drain into the Tennessee River. In the North Carolina mountains, the subspecies has not been collected in Tennessee River drainages and is known only from

the regions surrounding the headwaters of the New River, which flows into the Ohio, and the Atlantic draining Yadkin and Catawba Rivers.[3] Specimens have been examined as follows:

West Virginia: Wyoming Co., 1♂, 12 July 1947, H. H. Hobbs, Jr., and C. M. Wilson (USNM 1809). McDowell Co., 5 mi. E Iaeger, 1♂, 29 June 1950, L. Hubricht (RLH).

Virginia: Buchanan Co., 3 mi. SW Vansant, 1♂, 1♀, 1 July 1951, R. L. Hoffman and W. B. Newman (RLH). Russell Co., north slope of Clinch Mtn., 0.25 mi. E fire tower, 1♂, May 1974, D. W. Ogle (RLH). Washington Co., E side Clinch Mtn. near summit, 2 mi. N Mendota, 1♂, 31 July 1965, R. L. Hoffman and K. P. Brownell (RLH); woods along Va. hwy. 802, 3 mi. NE Mendota, 1♂, 31 July 1965, R. L. Hoffman and K. P. Brownell (RLH); and Straight Branch at Dripping Rock, near Damascus, 1♂, 1♀, 3 August 1941, S. T. Brooks (CM 52). Grayson Co., 1 mi. W Independence, 1♂, 18 June 1950, R. L. Hoffman and J. A. Fowler (RLH). Patrick Co., 2 mi. N North Carolina line, north of Mt. Airy, 1♂, 13 June 1937, L. P. Schultz and E. D. Reid (RLH).

Tennessee: Johnson Co. Backbone Rock Recreation Area, 4 mi. S Damascus, 3♂, 2♀, 11 July 1962, R. L. Hoffman (RLH).

North Carolina: Ashe Co., Mill Hill, 1♂, 31 July 1932, C. M. Breder (RLH). Alleghany Co., SE side of Roaring Gap on U. S. hwy. 21, 2♂, 1 May 1965, Radford College Expedition (RLH). Watauga Co., Boone, Campus of Appalachian State University, 1♂, 18 June 1948, M. Wright (RLH); and along Payne Branch Rd. between Boone and Blowing Rock, 1♂, 11 August 1962, H. F. Loomis (RLH). Wilkes Co., 1.5 mi. NW Wilbar, 2♂, 24 May 1958, L. Hubricht (RLH); 9 mi. NW Wilkesboro, Rendezvous Mtn., 8♂, 4♀, 25 July 1973, R. M. Shelley (NCSM 1854); 1 mi. S Oakwood, Brushy Mtns., 5♂, 5♀, 5 April 1952, L. Hubricht (RLH); 7.5 mi. E Wilkesboro, 2♂, 23 July 1950, L. Hubricht (RLH); and 9 mi. SE Wilkesboro, jct. N. C. hwy. 115 co. rd. 2428, 1♂, 2♀, 26 July 1973, R. M. Shelley (NCSM 1826). Caldwell Co., along U. S. hwy. 321, 8 mi. SE Blowing Rock, 1♂, 13 July 1962, R. L. Hoffman (RLH); and Hudson, 2♂, 1♀, 5 April 1952, L. Hubricht (RLH). Mitchell Co., Altapass, 3♂, several ♀, R. V. Chamberlin (RVC) (see footnote 3). Burke Co., 4 mi. SE Jonas Ridge, Barkhouse Recreation Area, 1♂, 11 July 1962, R. L. Hoffman (RLH); and 4 mi. N Morganton, 1♂, 3 October 1953, L. Hubricht (RLH). Davie Co., 4 mi. NE Mocksville, 1♂, 26 October 1952, L.

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[3] Altapass, the supposed type locality for *S. conclusa*, is near the headwaters of the North Toe River of the Tennessee River System, but it is also less than a mile from the divide with the Catawba River System in McDowell County. Both Dr. Hoffman (personal communication) and I have visited Altapass without finding *S. l. latior*, and it seems likely that the material in question actually came from across the divide in McDowell County and was labeled "Altapass" since this was the closet town. Chamberlin, who collected the specimens himself, was obviously confused about his location since he thought Altapass was in Tennessee! Thus, since Altapass is the only North Carolina locality within the Tennessee River System and since no additional specimens have ever been collected there despite several attempts, it is disregarded pending confirmation with fresh material.

Hubricht (RLH). Randolph Co., Ramseur, 1♂, 15 June 1954, H. E. Evans (RLH). Wake Co., William B. Umstead State Park, 1♂, 20 April 1973, R. M. Shelley (NCSM 1704). Franklin Co., 1.5 mi. S Pilot, near Mocassin Creek, 3♂, 2♀, 2 May 1959, L. Hubricht (RLH). Johnston Co., 2.8 mi. SW Clayton, 5♂, 18 April 1959, L. Hubricht (RLH); and 11.1 mi. SW Smithfield, along co. rd. 1330, 0.2 mi. N jct. N. C. hwy. 210, 3♂, 3 October 1972, R. M. Shelley (NCSM 1557).

Remarks: Hoffman (1950) noted that the West Virginia specimens are the northernmost in the genus *Sigmoria* and suggested an additional locality in north-central West Virginia (Lewis Co., near Jackson Mills), approximately 120 miles NE Pineville. This record was based on a female specimen, but as noted earlier, authentic records can only be based on mature males. Thus, the Lewis Co. locality should be deleted until confirmed by an adult male.

The identity of S. *aberrans*, described from Linville Falls, North Carolina, by Chamberlin (1939), is still somewhat in doubt. No county was given in the original description or by Hoffman (1950), but Chamberlin & Hoffman (1958) and Shelley (1975a) reported that the type-locality was in Avery Co. Although the Linville River, a tributary of the Catawba, arises in Avery Co., both the town of Linville Falls and the falls themselves are in adjacent Burke Co. The type locality for S. *aberrans* is therefore in Burke Co. rather than Avery.

The type-series of S. *aberrans* was comprised of "several males and females" (Chamberlin, 1939), but they are all now missing from their depository, the Chamberlin collection. No male topotypes are available either, although Hoffman (1950) refers to a topotype as being the key to the identification of a number of undetermined specimens of *Sigmoria*. This topotype, however, identified in his personal collection, is a female and unsatisfactory for species identification. Thus, no authentic male specimens of S. *aberrans* are available, and to further complicate matters, Chamberlin's description and illustrations (1939) are inadequate representations of the characters of the species. The color notations in the description, however, are typical of S. *l. latior*, and if a gonopod of this subspecies is examined by looking straight at the tip of the telopodite, the view vaguely resembles Chamberlin's sketch of S. *aberrans*. The best clue to the identity of S. *aberrans* is the specimen of S. *l. latior* from Burke Co., 4 mi. SE Jonas Ridge (RLH). This locality is approximately 5.5 mi. ESE Linville Falls and the closest available to the type-locality of S. *aberrans*. Thus, on the basis of this male and the few clues in Chamberlin's description (1939), it is concluded that S. *aberrans* is a flanged *Sigmoria* and conspecific with S. *l. latior*.

In selecting a specimen to redescribe the nominate subspecies, I chose without regard to locality and happened to pick the aforementioned male from Burke Co., 4 mi. SE Jonas Ridge. I did so because the specimen is one of the best available, is not broken, has both gonopods present, and typically represents the characters of the sub-

species. I wish to emphasize that the selection of this particular specimen for redescription of *S. l. latior* had nothing whatsoever to do with its proximity to the type-locality of *S. aberrans*.

In Chamberlin's 1939 paper, five species are originally described in *Sigmoria*, one of which, *S. divergens*, has since been transferred to *Cleptoria* (Hoffman, 1967), which Chamberlin also proposed in the same paper. Of the remaining four species, *S. aberrans* and *S. conclusa*, described consecutively, are identical, and two descriptions later is the conspecific *S. mariona*, here reduced to a subspecies. Thus, of the five species originally proposed in *Sigmoria*, only the type species, *S. munda*, remains intact. As with *S. aberrans*, the type-series of *S. conclusa* also consists of "several males and females," which, except for the male holotype, are in a jar of paratypes in the Chamberlin collection. These paratypes are badly fragmented, but there are three pieces with gonopods, two being *S. l. latior* and the other, a sigmoid form that is apparently undescribed! Thus, Chamberlin (1939) proposed consecutive synonyms, obscured the identities of both species through inadequate descriptions and illustrations, confused the type-locality of *S. conclusa* by placing it in Tennessee, and missed an undescribed species collected at the same time, not to mention the *Cleptoria* situation! This is perhaps somewhat extreme but nevertheless a not too atypical example of the type of confusion that exists in the pre-1950 literature on North American diplopods.

Sigmoria latior mariona Chamberlin, new status

Figure 4

Sigmoria mariona Chamberlin, 1939, p. 9, pl. 2, figs. 17, 18.—Hoffman, 1950, p. 6—Chamberlin & Hoffman, 1958, p. 50.—Wray, 1967, p. 152.

Type specimens: Male holotype and one male and two female paratypes collected by R. V. Chamberlin, 12 August 1910, from Marion, McDowell Co., North Carolina (RVC).

Diagnosis: Metaterga with yellowish stripes along caudal edge connecting with paranotal spots; male gonopods with following characters: prefemoral process bifurcate with vertical component usually much more prominent than horizontal component, although subequal in holotype; flange moderate, in depth (medial view) subequal to or slightly less than that of distal curvature of telopodite; subterminal tooth always absent; distal curvature of telopodite beginning approximately midway between apex and flange (or tooth location), forming arc with moderate diameter.

Variation: All specimens have a broad stripe along the caudal margin of the metaterga; accompanying notations indicate that the stripes and paranota are yellowish in life. On the gonopods, the two components of the prefemoral process are subequal in length in the holotype, but the vertical component is much larger in the Transylvania and Polk

Co. specimens. The depth of the flange relative to that of the distal curvature of the telopodite varies from subequal to a slightly more shallow flange. The latter condition is found on the Transylvania specimen and is due to the larger arc diameter formed by the distal curvature of the telopodite and not to a reduced flange. Absence of the subterminal tooth is the diagnostic feature of S. *l. mariona.*

Distribution: The subspecies has been collected only along the eastern edge of the mountains of southwestern North Carolina, in regions that drain into South Carolina and, eventually, the Atlantic Ocean. It has not been found west of the eastern continental divide in the French Broad River basin or other regions that drain into the Tennessee River. No specimens have been found in South Carolina, but S. *l. mariona* should be expected in the montane portions of Greenville and Pickens Counties. The low elevations of the three available specimens indicate that this subspecies is a valley form also. Specimens have been examined as follows:

North Carolina: McDowell Co., Marion, 2♂, 2♀, 12 August 1910, R. V. Chamberlin (RVC) HOLOTYPE and PARATYPES. Polk Co., Tryon, 1♂, March 1922, J. T. Nichols (RLH). Transylvania Co., Toxaway Gorge, 1100′, pine flat, 1♂, 3 August 1961, J. P. Paul (RLH).

Remarks: Hoffman (1950), Chamberlin & Hoffman (1958), and Wray (1967) all reported the Polk Co. locality as being the first definite record of S. *latior.* However, the specimen has the diagnostic characters of S. *l. mariona,* and the locality record is included here and not under the nominate subspecies.

Since both have a bifurcate prefemoral process, a comparison of S. *l. latior* and S. *l. mariona* is in order. The most obvious difference involves the subterminal tooth, which is present in the former and absent in the latter. They also differ in color pattern, with S. *l. mariona* being striped while the metaterga of S. *l. latior* are solid black in color. The distal portion of the telopodite of S. *l. mariona* is more broadly curved, with the curve beginning closer to the flange. The flange of the nominate subspecies tends to be squared, whereas that of S. *l. mariona* is more rounded. In overall length, the prefemoral process of S. *l. mariona* is longer, with a more obtuse angle between the base of the process and the tip of the vertical component. Some specimens of S. *l. latior* lack bifurcation, whereas all individuals of S. *l. mariona* display the trait, although the vertical component is much more prominent in the Polk and Transylvania specimens. Thus, S. *l. mariona* is quite different from S. *l. latior* and exhibits similarities to the South Carolina subspecies, which will be discussed in the following section.

Sigmoria latior hoffmani, new subspecies

Figure 5

Type specimen: Male holotype collected by L. Hubricht, 14 May 1960, from upland mixed woods, 4.4 mi. NW North, Orangeburg Co.,

South Carolina (RLH). The subspecies is named after Richard L. Hoffman, in recognition of his contributions to the taxonomy of North American diplopods and his generous assistance to me, including the loan of all available material of this subspecies.

Diagnosis: Metaterga with yellowish stripes along caudal edge connecting with paranotal spots; male gonopods with following characters: prefemoral process simple, not bifurcate, angle between base and tip greater than 90°; flange greatly enlarged, extending (medial view) to level of prefemoral process, greater in depth than that of distal curvature of telopodite; subterminal tooth present but variable; distal curvature of telopodite beginning closer to tooth than to tip of telopodite, forming arc with relatively broad diameter.

Variation: All specimens have a broad stripe along the caudal edge of the metaterga; accompanying notations indicate that the stripes and paranota are yellowish in life. On the gonopods, the size of the flange varies and is largest in the southernmost individuals with the largest being on the males from Colleton Co. The most variable character is the subterminal tooth, which is sharply pointed on the Charleston Co. specimens and is a low, flat callus on a male from Berkeley Co. The tooth on the holotype is intermediate between these extremes, and no pattern is evident to the tooth variation. The distal curvature of the telopodite is narrowest in the Charleston specimens but is still greater than that of the other subspecies.

Distribution: The subspecies appears to be restricted to the coastal plain of southern South Carolina, between the Savannah and Congaree-Santee Rivers; intergrades have been collected from across the Santee in Williamsburg Co. and the Congaree in Richland Co. Specimens have been examined as follows:

South Carolina: Lexington Co., Swansea, 1♂, 23 December 1951, L. Hubricht (RLH); and Pelion, 1♂, 17 April 1954, L. Hubricht (RLH). Berkeley Co., near diversion canal on S. C. hwy. 45, SW Pineville, 2♂, 13 June 1959, L. Hubricht (RLH). Charleston Co., swamp, 1.5 mi. S Adams' Run, 5♂, 1♀, 5 July 1959, L. Hubricht (RLH). Orangeburg Co., upland mixed woods, 4.4 mi. NW North, 1♂, 14 May 1960, L. Hubricht (RLH) HOLOTYPE. Bamberg Co., Lemon Swamp, 2.2 mi. S Bamberg, 1♂, 21 November 1959, L. Hubricht (RLH). Colleton Co., 5 mi. N Yemassee, 2 ♂, 2♀, 10 June 1963, D. R. Whitehead (RLH).

Remarks: This subspecies differs from the nominate subspecies in color pattern and most gonopodal characters, and it exhibits the extreme in development of the flange and distal curvature of the telopodite. It resembles S. *l. mariona* in color pattern, and the prefemoral processes of the gonopods of the two subspecies are similar in length, with a more obtuse angle between the base and tip than in S. *l. latior*. The subterminal tooth, absent in S. *l. mariona*, is variable in S. *l. hoffmani* and much reduced in some individuals. The distal curvature of the

FIGS. 15–16. Left male gonopods of *Sigmoria latior* intergrades (medial view) with direct view of flange. 15, *S. l. latior* × *S. l. mariona,* specimen from 2.2 mi. SE Dysartsville, McDowell Co., N. C. (RLH). 16, *S. l. latior* × *S. l. hoffmani,* specimen from Raeford, Hoke Co., N. C. (RLH).

telopodite, beginning midway between the flange (tooth location) and tip in *S. l. mariona,* begins closer to the tooth in *S. l. hoffmani.* The flange of *S. l. hoffmani,* while larger than those of the other two subspecies, resembles that of *S. l. latior* in its squarish configuration. Relationships between the three subspecies will be discussed in the concluding section.

INTERGRADES

As shown in the distribution map (Fig. 17), a large zone of intergradation occurs in the region of the central Carolinas, around their common border. The gonopods of the intergrades vary, depending upon the relative expression of the characters of each subspecies, but all known specimens display the striped color pattern of *S. l. mariona* and *S. l. hoffmani.* Only a small number of intergrades are available, and none have been collected which could be interpreted as displaying characters of all three subspecies.

S. l. latior × *S. l. mariona*

The one available specimen resembles *S. l. mariona* in color pattern, size and shape of the flange, and distal curvature of the telopodite. It

resembles S. *l. latior* in the prefemoral process and subterminal tooth; the latter, however, is reduced from the condition in the nominate subspecies. Locality data are as follows: North Carolina, McDowell Co., 2.2 mi. SE Dysartsville, 2♂, 1♀, 19 September 1953, L. Hubricht (RLH).

S. *l. latior* × S. *l. hoffmani* (hereafter abbreviated *l* × *h*)

The specimens from this zone of intergradation possess gonopods that are generally intermediate between the two subspecies. There is usually some bifurcation of the prefemoral process, but the structure is intermediate in overall length and angulation. Both the distal curvature of the telopodite and depth of the flange are also intermediate. The subterminal tooth, however, conforms more to the condition in S. *l. latior*. As mentioned previously, all specimens are striped (an S. *l. hoffmani* trait), but the color varies as in S. *l. latior*, being yellow in the Morrow Mountain specimens and pink in those from Scotland Co.

The range of intergradation extends roughly from the Deep-Cape Fear Rivers of North Carolina to the Congaree-Santee Rivers of South Carolina. Individuals are known from as far west as the Uwharrie Mtns., North Carolina, from Morrow Mountain State Park. Specimens have been examined as follows:

North Carolina: Stanly Co., Morrow Mtn. State Park, 1♂, 31 July 1951, T. Cohen (RLH); and 5♂, 2♀, 9 August 1973, R. M. Shelley (NCSM 1891). Moore Co., 4.4 mi. SW Robbins, along N. C. hwy. 24, 0.5 mi. W jct. co. rd. 1276, 1♂, 24 April 1973, R. M. Shelley (NCSM 1729). Hoke Co., Raeford, 1♂, 1♀, 22 March 1952, L. Hubricht (RLH). Scotland Co., 3.7 mi. NW Wagram, 4♂, 8 October 1974, J. E. & M. R. Cooper (NCSM 2538). Unknown Co. (restricted to S of Deep-Cape Fear Rivers) and date, 1♂, collector unknown (MNHP) HOLOTYPE of *Fontaria latior*.

South Carolina: Richland Co., 1♂, 26 April 1963, B. Power (RLH); and 2♂, 4♀, May 1963, M. Byrd (RLH). Williamsburg Co., near Santee River on S. C. hwy. 41, 12.5 mi. SSW Andrews, 2♂, 13 June 1959, L. Hubricht (RLH).

S. *l. mariona* × S. *l. hoffmani* (hereafter abbreviated *m* × *h*)

No specimens have yet been taken that are intermediate between these two subspecies. They should be expected, however, in the western piedmont of South Carolina, perhaps around Greenville and Spartanburg. The absence of material is particularly unfortunate in view of the morphological similarities between the two subspecies, and future collecting should be concentrated in the probable area of intergradation.

Ecology

Little can be said about the ecology or specific habitat requirements of these subspecies. Most of the loaned material lacked this informa-

tion, but I can report on the material which I collected. One point of interest is the relative abundance of the nominate subspecies in the western and eastern piedmont of North Carolina. In four years' of surveying the eastern piedmont diplopods, in all habitats at all seasons, only four males have been discovered: three in Johnston Co. (NCSM 1557) and one in William B. Umstead State Park, Wake Co. (NCSM 1704). Conversely, in a three-day summer field trip to Wilkes Co., in the northwestern piedmont and foothills, 11 males and 10 females were collected, and at one locality a number of individuals were examined but not retained. This apparent disparity in relative abundance might be due to habitat differences, with the foothills of Wilkes Co. being more desirable in terms of thickness of the humus layers, temperature, humidity, and other factors. The humus layers are noticeably thinner in the eastern piedmont, and the frequent periods of hot, dry weather render all diplopods scarce, not just males of *Sigmoria.*

As for specific habitat characteristics, most of the millipeds are found in the same habitats as xystodesmids in general—under rocks, logs, and in litter and humus layers of predominantly hardwood localities. Notations accompanying the specimens of *S. l. hoffmani,* however, indicate that 9–11 individuals were collected from swamps or swampy habitats. The southeastern swamps and coastal plain are not generally regarded as preferred habitats for xystodesmids, but one other genus known from the region is *Stelgipus,* reported by Chamberlin & Hoffman (1958) from Wadmalaw Island, Charleston Co.

Some of the North Carolina specimens came from habitats which are different enough to warrant specific attention. The male from William B. Umstead Park (NCSM 1704), for example, was found dead, apparently drowned, in a pool of water in a pine-hardwood locality. The specimens from Johnston Co. (NCSM 1557) were found in a rather unlikely habitat, on sandy soil under a thin layer of leaves. This same locality has yielded *Apheloria* and immatures of *Nannaria,* probably *N. conservata,* as well as *Ptyoiulus* (Shelley, 1975b). In Scotland Co., four males, $l \times h$ intergrades (NCSM 2538) were discovered under a log near a burned house overgrown with weeds. All other specimens were collected in habitats that are typical for xystodesmid millipeds.

Distribution

Sigmoria latior ranges from the mountains of southern West Virginia to the Savannah River region of coastal South Carolina (Fig. 17), a distance of roughly 400 miles. In Virginia and West Virginia, the range is narrow, but it widens considerably in the Carolinas, the area of major concentration. There it becomes triangular in shape with S. *l. latior* in the north, S. *l. mariona* in the southwest, S. *l. hoffmani* in the south, and intergrades centrally. The distributional pattern could aptly be described as the Carolinas, with a northwestward projection into southern West Virginia. Specific ranges for the three subspecies are as follows:

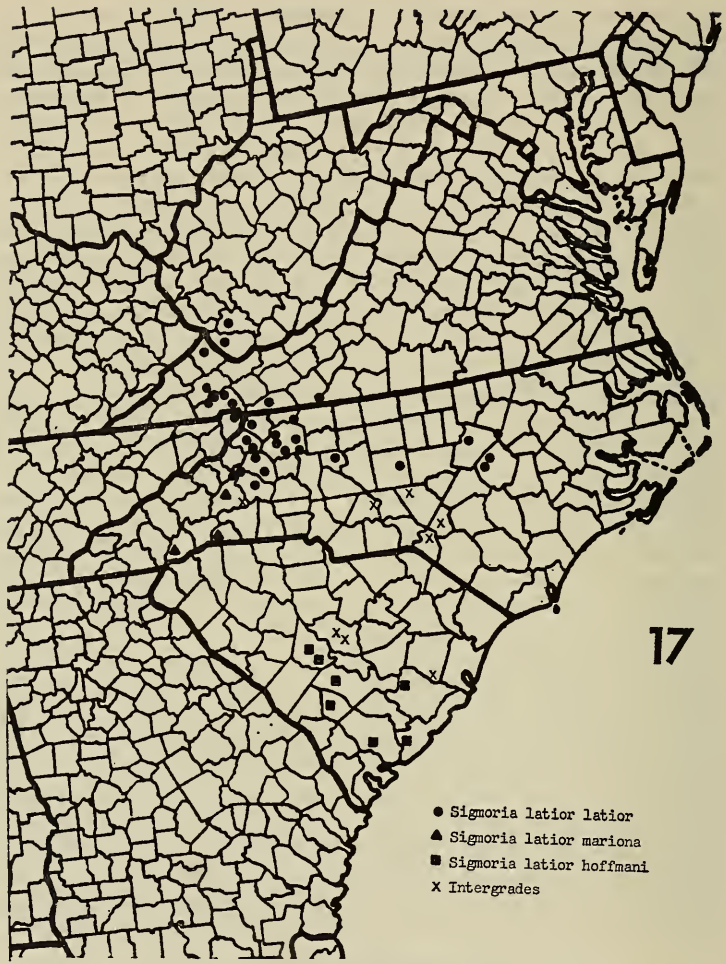

FIG. 17. Distribution of *Sigmoria latior* in eastern United States.

latior—northern piedmont and mountains of North Carolina, north of the Deep-Cape Fear and Catawba Rivers, through southwestern Virginia to southern West Virginia.

mariona—eastern mountain slope (Atlantic drainages) of southwestern North Carolina.

hoffmani—coastal plain of southern South Carolina, between the Savannah and Congaree-Santee Rivers.

Several points about the distribution are noteworthy. First, rivers

and drainage basins are important factors influencing the ranges of the subspecies; they effectively form boundaries for both S. *l. latior* and S. *l. hoffmani.* Disparities in distribution in individual river systems are also intriguing. For example, the nominate subspecies is common in the upper New River basin in northwestern North Carolina, but it has not been encountered along the New River in the Ridge and Valley Province of Virginia, one of the most thoroughly collected areas in the southeast (Hoffman, 1969). Also, except for specimens of S. *l. latior* from localities near the Clinch and Holston Rivers in Virginia, no adult males have been authentically taken from localities that drain into the Tennessee River. In Watauga Co., North Carolina, two individuals have been collected from localities near the headwaters of the New River, but none have been found in the Watauga basin, only a few miles away. Likewise, S. *l. mariona,* in southwestern North Carolina, is known only from the Atlantic drainages along the eastern mountain slope and has not been encountered in the French Broad basin, just across the eastern continental divide. Although lack of adult males may partially explain this absence, it is also true that considerable field work has been carried out in the Tennessee drainages. If males are present in numbers at all similar to those in neighboring basins, it seems that at least one would have been discovered by now. The absence of S. *latior* from the Great Smoky Mountains, to cite one specific region, is considered more real than artificial, since it too is one of the best collected areas in the southeast (Hoffman, 1969). The mountains and valleys of the Tennessee River System abound in climax forests with thick humus layers, so the absence cannot be due to unsuitable habitat. Instead, it seems that the pattern can best be attributed to two factors: altitude restrictions and competition.

Hoffman (1950) suggested that the species might be a valley form despite its occurrence in a mountainous region. Although he was speaking primarily for northwestern North Carolina and adjacent Virginia, it now appears that the observation is valid for all montane forms of the species. In elevation, the species ranges from near sea level in coastal South Carolina (S. *l. hoffmani*), to approximately 3018 ft. near the summit of Clinch Mtn., Washington Co., Virginia (S. *l. latior*). Nowhere does it approach the high mountain peaks, and most of the material was collected in river valleys. This preference for valleys may partially explain the absence from the Tennessee drainage; in order to cross the eastern continental divide, it would have to ascend intervening higher elevations.

Throughout much of its range, S. *latior* is the only known *Sigmoria* present. Several additional species, however, occur in the mountains of the Tennessee River System, including the abundant S. *nantahalae* in areas surrounding the headwaters of the Nantahala (Little Tennessee) and Hiwassee Rivers (Hoffman, 1958). It thus seems that competition

with these species or even other diplopods could partially explain the distributional pattern.

In a different region, no individuals have been found in the Tar and Roanoke River basins of piedmont North Carolina. I have collected extensively in these regions, but *Apheloria* is the only xystodesmid found. In this case, the reason might be lack of suitable habitat. Much of the area around Kerr and Gaston Lakes (impoundments of the Roanoke River) and the upper Tar River basin was once cotton farmland that is now reverting back to forests and is currently in pine stages of succession. Tracts of hardwoods or even mixed hardwoods and pine are rare, whereas they are more plentiful in the upper Neuse River basin, where all eastern piedmont specimens of *S. l. latior* have been found.

The nominate subspecies has also not been encountered in piedmont Virginia. In this case, however, so little field work has been carried out that I cannot state with any degree of confidence that the absence is real.

A final distributional note involves the two distinct color patterns (Figs. 1, 2). The striped subspecies, *S. l. mariona* and *S. l. hoffmani*, are the southernmost, while *S. l. latior*, with solid black metaterga, occupies the northern half of the range. The dividing line between the two patterns coincides closely with the southern border of distribution for *S. l. latior*, and all the intergrade material is striped, regardless of location. Color pattern alone, therefore, restricts a specimen to either half of the range.

Relationships

Relationships of *S. latior* with other species of Sigmoria cannot be inferred at this time. Within the species itself, the nominate subspecies is morphologically the simplest and the form closest to a more primitive ancestor. In the flange and distal curvature of the telopodite, *S. l. latior* represents the simplest condition, while *S. l. hoffmani* displays the extreme development of each structure. The third subspecies, *S. l. mariona*, is intermediate in both of these characters, and the loss of the subterminal tooth appears to be a secondary modification. The geographical evidence suggests an origin in northwestern North Carolina, with migration northwestward to West Virginia and southward-eastward in North Carolina and into South Carolina. Although *S. l. mariona* is intermediate between *S. l. latior* and *S. l. hoffmani*, it is uncertain whether the latter evolved from *S. l. mariona* or directly from the nominate subspecies, since expansions toward South Carolina and southwestern North Carolina are believed to have occurred concurrently. Of highest priority now are collections in the Greenville-Spartanburg region, for $m \times h$ intergrades, and in piedmont Virginia, to determine if yet another subspecies occurs in that region.

Literature Cited

Attems, Carl G. 1938. Polydesmoidea 11. Das Tierreich No. 69: 1–487.

Brölemann, Henri W. 1900. Myriapodes d'Amerique. Mem. Soc. Zool. France 13:89–131.

Chamberlin, Ralph V. 1939. On some diplopods of the family Fontariidae. Bull. Univ. Utah Biol. Ser. 30:1–19.

——— and Richard L. Hoffman. 1958. Checklist of the millipeds of North America. Bull. No. 212, U. S. Natl. Mus. 236 pp.

Hoffman, Richard L. 1949. Nine new xystodesmid millipeds from Virginia and West Virginia, with records of established species. Proc. U. S. Natl. Mus. 99:371–389.

———. 1950. American polydesmoid millipeds of the genus *Sigmoria*, with notes on distribution. Am. Mus. Novitates No. 1462: 1–7

———. 1958. A new milliped of the genus *Sigmoria* from western North Carolina. Proc. Ent. Soc. Wash. 60:281–285.

———. 1967. Revision of the milliped genus *Cleptoria* (Polydesmida:Xystodesmidae). Proc. U. S. Natl. Mus. 124:1–27.

———. 1969. The origin and affinities of the southern Appalachian diplopod fauna. Pp. 221–246 *in* P. C. Holt (ed.) The Distributional History of the Southern Appalachians, Part 1: Invertebrates. Res. Div. Mongr., Virginia Polytech. Inst., Blacksburg, Virginia.

Levi, Herbert W., Lorna R. Levi, and Herbert S. Zim. 1968. A Guide to Spiders and their Kin. Golden Press, New York, 160 pp.

Shelley, Rowland M. 1975a. An interesting relationship in the diplopod genus, *Sigmoria* (Polydesmida:Xystodesmidae). ASB Bull. 22:78–79 (Abstract).

———. 1975b. The identity of *Nannaria conservata* Chamberlin, with notes on an abnormal male and descriptions of two new species of *Nannaria* from North Carolina (Diplopoda:Polydesmida: Xystodesmidae). Proc. Biol. Soc. Wash. 88:179–188.

Wray, David L. 1967. *Insects of North Carolina, Third Supplement.* North Carolina Department of Agriculture, Division of Entomology, Raleigh, 181 pp.